Digger wasps (Hymenoptera, Sphecidae) in Burmese amber

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SYNOPSIS. The following new taxa of the family Sphecidae are described from Upper Cretaceous Burmese amber: *Burmastatus triangularis* gen. et sp. nov. and *Cirrosphex admirabilis* gen. et sp. nov., are members of the new subfamilies Burmastatinae and Cirrosphecinae; *Apodolichurus sphaerocephalus* gen. et sp. nov., *A. diaphanus* sp. nov., *Cretampulex gracilis* gen. et sp. nov., and *Mendampulex monilicularis* gen. et sp. nov. are members of the new ampulicine tribes, Apodolichurini, Cretampulicini, and Mendampulcini, respectively; *Prolemistus apiformis* gen. et sp. nov. and *Cretospilomena familiaris* gen. et sp. nov., are placed in the tribe Pemphredonini. *Trigonalys pervetus* Cockerell, 1917, originally described in the family Trigonalyidae, is moved to the new sphecid genus *Trigampulex* gen. nov., *incerta sedis*. The principal differences of the evolution of the wing venation between the Upper Cretaceous and recent sphecid wasps are discussed.

INTRODUCTION

Until now the Apocrita were represented only by the families Aulacidae, Bethylidae, and Trigonalyidae in Upper Cretaceous amber from Myanmar (Cockerell, 1917*a*, 1917*b*, 1917*c*, 1917*d*, 1920) [though the Myanmar Trigonalyidae are now attributed to Sphecidae – see below]. During a brief study of fossil insects in the Department of Palaeontology of The Natural History Museum (London, UK), Prof. A.P.Rasnitsyn (Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia) identified some Burmese amber samples including, among many other arthropods, several sphecid wasps. This material is treated herein.

It is necessary to note that the preparation quality, the transparency of the samples and the position of the inclusions inside the samples are highly heterogeneous, and the necessity to maintain the initial state of the samples has considerably limited the opportunities of thorough analysis of the inclusions because of inaccessibility to study some highly important features. Undoubtedly, this has affected the completeness of the descriptions of the new taxa presented here.

Though in recent years some authors have divided Sphecidae into several separate families on the basis of cladistic analysis, I cannot consider for the present that their preliminary results carry complete conviction. Here I follow the traditional view that Sphecidae are an indivisible family of hymenopterous insects, taking into account that it may be a paraphyletic grouping. I have tried to use the majority of the diagnostic characters and terms accordingly the generic revision of the recent sphecid wasps (Bohart & Menke, 1976) to preserve the continuity and comparativeness of the taxa. At the same time, the designation of the scutal lines is given according to the well reasoned, from my point of view, proposals of Budrys (Budrys & Kazenas, 1992; Budrys, 1993).

Specimens were examined under a Zeiss-stereomicroscope in a thick sugar solution rather than immersion oil in order to minimize the possibility of damage.

SYSTEMATIC DESCRIPTIONS

Superfamily **APOIDEA** Family **SPHECIDAE**

I. New subfamilies of Sphecidae

The family Sphecidae was divided into 11 subfamilies in the revision of recent genera (Bohart & Menke, 1976). In recent years some authors have included the genera of the subfamily Larrinae (sensu Bohart & Menke, 1976) in the subfamily Crabroninae (e.g., Menke & Fernández, 1996). Furthermore, following conception of the indivisible family Sphecidae, the genus *Heterogyna* Nagy, 1969, as well as the genera *Dolichurus* Latreille, 1809, *Paradolichurus* Williams, 1960, *Aphelotoma* Westwood, 1841, *Austrotoma* Riek, 1955, *Trirogma* Westwood, 1841, and *Ampulex* Jurine, 1807, which were included into separate families in a review of the families of Hymenoptera (Goulet & Huber, 1993), should be attributed to the subfamilies Heterogynainae and Ampulicinae.

Fossil sphecid wasps have been already described in the following recent subfamilies: Ampulicinae (Nemkov, 1988), Sphecinae (Cockerell, 1906, 1907; Menke & Rasnitsyn, 1987), Pemphredoninae (Cockerell, 1906; Rohwer, 1909; Evans, 1969, 1973; Sorg, 1986; Budrys, 1993), Crabroninae (Cockerell, 1908, 1909, 1910; Rohwer, 1908; Antropov & Pulawski, 1989, 1993; Prentice & Poinar, 1993; Antropov, 1995), Bembicinae (Cockerell, 1906, 1922; Rohwer, 1908; Pulawski & Rasnitsyn, 1980, Nemkov, 1990), and Philanthinae (Cockerell, 1906; Rohwer, 1909; Timon-David, 1944). The Lower Cretaceous genera Angarosphex Rasnitsyn, 1975, Baissodes Rasnitsyn, 1975, Oryctobaissodes Rasnitsyn, 1975, Trichobaissodes Rasnitsyn, 1975, and Bestiola Pulawski et A.Rasnitsyn, 1999 have been assigned to the fossil sphecid subfamily Angarosphecinae (Rasnitsyn, Pulawski & Martínez-Delclòs, 1999). Furthermore, the subfamilial position has not been ascertained for Archisphex Evans, 1969, Taimyrisphex Evans, 1973, and Cretosphex A.Rasnitsyn, 1975 (Rasnitsyn, 1980).

Subfamily BURMASTATINAE nov.

TYPE GENUS. Burmastatus gen. nov., here designated.

DIAGNOSTIC FEATURES.

- 1. Inner eye orbits straight, parallel; ocelli simple.
- Antennae attached to lower part of face; antennal sockets touching clypeal base; female antennae 12-segmented; scapes modified into large triangular plate with elongate ventral part.
- 3. Clypeus transverse, short.
- 4. Mandibles without preapical teeth, with obtuse angle externoventrally and obtuse flat inner prominence basally; mandible sockets open; palpal formula 6–4; mouthparts short.
- 5. Pronotal collar short, flattened dorsally, with sharp transverse keel; pronotal lobes almost touching tegulae.
- 6. Scutum with adlateral (=parapsidal) lines, reaching at least 2/3 of scutal length; admedian lines not expressed.
- 7. Mesopleuron with incomplete straight episternal sulcus; omaulus, subomaulus, sternaulus, and acetabular carina absent, scrobal sulcus developed.
- 8. Metapleuron completely developed.
- 9. Midtibia with two apical spurs; midcoxae subcontiguous; hindcoxae contiguous; precoxal lobes present; hindfemur apically simple; tarsal claws simple.
- 10. Propodeum short (shorter dorsally than posteriorly); propodeal dorsal enclosure U-shaped, concave, broader than long; propodeal lateral carinae present; intercoxal carinae absent.
- 11. Forewings with two submarginal and two discoidal cells; marginal cell very short, with acute apex touching wing margin; recurrent vein I received by submarginal cell I, recurrent vein II received by submarginal cell II; forewing media diverging beyond cu-a.
- 12. Hindwing jugal lobe narrow, longer than 2/3 of submedial cell length; hindwing media diverging before cu-a; M distinctly longer than r-m and Rs together; Sc and A₁₋₂ absent.
- 13. Abdomen without petiole; tergite I with lateral carinae; pygidial plate absent.

COMPARISONS. The new subfamily resembles Ampulicinae in having developed adlateral lines and two apical midtibial spurs, but differs by the simple tarsal claws and the mandibles with an obtuse externoventral angle. Combination of the last two features with two apical midtibial spurs is characteristic for the subfamilies Astatinae and Xenosphecinae, although these have no adlateral lines. The new subfamily also resembles representatives of Astatinae in having a long jugal lobe (it is short in Xenosphecinae), but differs in the venation of the fore- (particularly by the short marginal cell with its acute apex touching forewing margin) and hindwings (particularly of the medial cell), by the short propodeum, and by lacking the pygidial plate.

REMARKS. The form of the pronotum (particularly of its collar, lobes, and lower angles) and of the hindtibial brush shows that the specimen belongs to the Sphecidae, but its main diagnostic features (presence of the adlateral lines, two apical midtibial spurs, obtuse externoventral angle of mandibles, and simple tarsal claws) do not relate it to any recent subfamily of Sphecidae. The considerably specialized fore- and hindwing venation differs from the known fossil genera *Angarosphex*, *Archisphex*, *Cretosphex*, and *Taimyrisphex*. Such distinct apomorphies as the scape modified into large, vertical, triangular plates, considerably diminished forewing marginal cell with its acute apex touching the wing margin, and the hindwing M being longer than r-m and Rs combined, place this specimen as the representative of a new subfamily. It is necessary to mention, that among recent sphecids the similar form of the hindwing

medial cell apex is typical for almost all Oxybelini and Crabronini, for some genera of Miscophini (in *Saliostethus* Brauns, 1897, and *Saliostethoides* Arnold, 1924 and, to a smaller degree, in *Miscophus* Jurine, 1807, *Miscophoides* Brauns, 1897, and *Auchenophorus* Turner, 1907), and also for some Pemphredonini (as the steps in *Ammoplanus* Giraud, 1869, and *Ammoplanellus* Gussakovskij, 1931, and distinctly in *Pulverro* Pate, 1937). The postfurcal cu-a is found only in the last genus. The reduction of the forewing venation in these groups, which is likely related in the last two tribes to the considerable diminution of the body size, has a very different nature (truncation and reduction or, on the contrary, elongating of the marginal cell; complete or partial reduction of the submarginal cell II, owing to reduction of its outer vein or petiolization; enlarging of the stigma). Consequently, this superficial similarity was, undoubtedly, acquired independently in each group.

Genus BURMASTATUS nov.

ETYMOLOGY. The generic name is derived from the toponym Burma and the generic name *Astata*. The name is masculine.

TYPE SPECIES. *Burmastatus triangularis* sp. nov., here designated; the only species.

DIAGNOSIS. Inner eye orbits parallel; ocelli simple; antennal sockets touching clypeal base; female antennae 12-segmented; scapes modified into large triangular plate; clypeus transverse, short; mandibles without preapical teeth, with obtuse angle externoventrally and obtuse flat inner prominence basally; mandible sockets open; palpal formula 6-4; mouth parts short. Pronotal collar short, flattened dorsally; pronotal lobes almost touching tegulae; scutum with adlateral and admedian lines; mesopleuron with incomplete straight episternal sulcus, not reaching their anterior margin; omaulus, subomaulus, sternaulus, and acetabular carina absent, scrobal sulcus developed; midtibia with two apical spurs; midcoxae subcontiguous; hindcoxae contiguous; precoxal lobes present, short; hindfemur apically simple; tarsal claws simple. Forewings with two submarginal and two discoidal cells; marginal cell very short, with acute apex touching wing margin; recurrent vein I received by submarginal cell I, recurrent vein II received by submarginal cell II; forewing media diverging beyond cu-a. Hindwing jugal lobe narrow, longer than 2/3 of submedial cell length; hindwing media diverging before cu-a; M distinctly longer than r-m and Rs together. Propodeum shorter dorsally than posteriorly; propodeal dorsal enclosure Ushaped, concave, broader than long; propodeal lateral carinae present; intercoxal carinae absent. Abdomen without petiole; tergite I with lateral carinae; pygidial plate absent.

Burmastatus triangularis sp. nov.

Figs 1–6

ETYMOLOGY. The species name is derived from the Latin masculine adjective *triangularis*, meaning 'triangular'; the name is a reference to the shape of the female scape.

HOLOTYPE. Department of Palaeontology of The Natural History Museum (London), In.20197; partly preserved female specimen (the following parts are absent: left antennomeres 4–8, the largest part of the left eye, left mandible basally, the largest part of the both left wings from the base, outer side of the left forefemur, left mid- and hindfemora medially, left lateral side of the abdomen, distal parts of the both right wings, and partly the posterior part of the right forewing; left posterolateral side of the abdomen is damaged; distal part of the right forewing considerably and scutellum, postscutellum, and propodeal dorsal side from the left partly deformed) in a polished



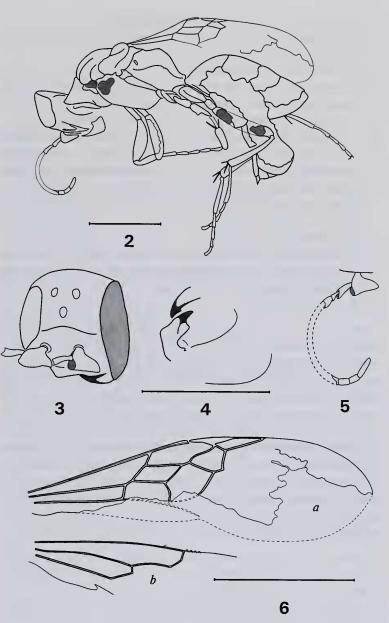
Fig. 1 *Burmastatus triangularis* gen. et sp. nov., holotype, In.20197, female, Burmese amber. Length 3.2 mm.

triangular-round sample of Burmese amber (probably Upper Cretaceous).

DESCRIPTION. Female. Head rounded, weakly flattened; pronotum moderately elongate, with flattened convex collar, prolong lateral ridges, and sharp keel along posterior margin; scutum strongly convex anteriorly, considerably higher than pronotal posterior margin, straight posteriorly; scutellum strongly roundly convex, twice as short as scutum; postscutellum flat, twice as short as scutellum; mesopleuron convex, episternal and scrobal sulci present; metapleuron with broadly separated metapleural pits and weakly expressed metapleural flange; midcoxae with two, hindcoxae with only external carinae; fore trochanters elongate, mid- and hindtrochanters simple; main part of forewing vein placing in proximal half of wing; hindwings with a row of 4 hamuli; propodeal dorsal area with wide enclosure reaching 2/3 of its length from base; propodeal lateral sides outlined dorsally by lateral carinae, ending anteriorly below oval spiracles; propodeal hind side outlined dorsally by curved carinae; abdominal tergite I shorter than wide, with thin medial furrow anteriorly.

Mandible ventrally and labrum with very long bristles; pronotum and scutum covered with very short erect and partly semi-adjacent hairs; mesopleuron ventrally covered with hairs, which length equal to hind basitarsus thickness; forecoxae ventrally covered with erect hairs 1.5 times longer than apical antennomere thickness; tibiae with dense short semi-adjacent hairs and with considerably longer and thicker outer spines lengthening towards apices, sparse on fore- and most dense on hindtibiae; fore tarsomeres with dense and short semiadjacent hairs and sparse apical and longer lateral spines, one of which on I–III tarsomeres longer than following tarsomere, though real rake absent; mid- and hind tarsomeres with dense and short semi-adjacent hairs and with apical spines thinner than those on fore tarsomeres and ventral spines approximately 2 times shorter than those on fore tarsomeres. Body surface weakly sculptured, without distinct punctures, with visible surface dull.

Yellowish-red palpi, scape, head ventrally, mesopleuron anteriorly and ventrally, legs completely, and large medial spot on abdominal tergite I. Brown antenna, mandible mainly, pronotum, scutum laterally and along adlateral lines, scutellum, mesopleuron dorsally and laterally, metapleuron, wing veins, propodeum laterally, and abdomen



Figs 2-6 Burmastatus triangularis gen. et sp. nov., holotype, In.20197, female, Burmese amber. 2, Total view laterally. 3, Head, dorsolaterally.
4, Mandibles ventrolaterally. 5, Left antenna laterally; 6, Right wings (a – forewing, b – basal fragment of hindwing). Scale bars = 1 mm.

mainly. Black mandible apically, occiput, scutum medially, propodeal dorsal enclosure and hind side, and abdominal tergite III medially. Body length 3.2 mm. The male is unknown.

Subfamily CIRROSPHECINAE nov.

TYPE GENUS. Cirrosphex gen. nov., here designated.

DIAGNOSTIC FEATURES.

- 1. Antennal sockets covered dorsally by separated frontal prominences.
- 2. Occipital carina forming a complete circle, almost touching hypostomal carina.
- 3. Mandible without externoventral angle or notch, with inner preapical tooth, curved forward (slightly prognathous).
- 4. Palpi not elongate; palpal formula 6–4.
- 5. Male antenna 13-segmented; flagellomeres (except apical article) posteriorly with flat triangular prominences, longest on flagellomeres 5–9.
- 6. Pronotum short, straight posteriorly.

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- 7. Adlateral lines reaching scutal posterior margin.
- 8. Midcoxae distinctly separated, with dorsolateral ridge.
- 9. Midtibia with one apical spur.
- 10. Hindfemur simple apically.
- 11. Tarsi simple, plantulae absent, tarsal claws probably with a tooth, arolium not shorter than claw.
- 12. Propodeum not elongate, rounded, without lateral carinae.
- 13. Forewings with 3 submarginal cells (I and II almost equal in size, III smallest) and two discoidal cells; both recurrent veins received by submarginal cell II; marginal cell large, with acute apex touching wing margin; forewing media diverging beyond cu-a.
- 14. Hindwing jugal lobe small, rounded; hindwing media diverging before cu-a.
- 15. Abdomen without separate petiole and with 7 visible segments; tergite I with lateral carina; sternite I with medial ridge; tergite VII sharp.
- 16. Cerci absent.

COMPARISONS. The new subfamily differs from recent sphecid subfamilies, excluding Ampulicinae, by the well developed, long adlateral lines and dentate tarsal claws. Among the representatives of Ampulicinae the new subfamily resembles the fossil *Protodolichurus* Nemkov, 1988 (Dolichurini) in having separated frontal prominences above the antennal bases, a short pronotal collar, a more or less rounded propodeum, and completely visible abdominal segments. It also resembles the recent genera *Trirogma* Westwood, 1841 (Dolichurini) in having no cerci and a sharply prominent clypeus bearing a medial ridge. Cirrosphecinae subfam. nov. differs from Ampulicinae most notably by the single midtibial spur, very short and low pronotal collar, expressed episternal sulcus, and also by the pectinate flagellum.

REMARKS. The form of the pronotum (short collar with a straight posterior margin and distinct pronotal lobes) and of the hindtibial cleaning brush shows that the specimen belongs to the Sphecidae. It is similar to Ampulicinae by the adlateral lines and dentate tarsal claws [the studied specimen has a visible tooth only on the inner claw of the right hindtarsus (the rest of the claws are completely covered by foreign particles or blebs)], which are the diagnostic features for the last, and also by the prognathously curved mandibles, which are usual for the females of *Ampulex*. As for the form of the mandible, some males of recent Sphecidae often have considerably stronger modified mandibles, and their form may be considered to be a sexual signal. The expressed frontal prominences above the antennal sockets also occurs outside the Ampulicinae [for example, both single and separated prominences are usual in some species-groups of the genus *Trypoxylon* Latreille, 1796 (Crabroninae, Trypoxylini)].

Distinctive features, which are not characteristic for Ampulicinae, are the form of the flagellomeres, the reduction of the 2nd apical midtibial spur, the contiguous hindcoxae, the strongly enlarged submarginal cell II and diminished submarginal cell III, the delicately sculptured propodeum without lateral carinae, and the elongate first abdominal segment bearing a medial ridge on the sternite. Probably, a more detailed study of the specimen will give additional characters substantiating its isolation as a separate subfamily (unfortunately, in its present state the sample is open for study only from a certain visual angle on its left side).

Genus CIRROSPHEX nov.

ETYMOLOGY. The generic name is derived from the Latin noun *cirrus*, meaning 'fringe', and the generic name *Sphex*. The name is masculine.

TYPE SPECIES. *Cirrosphex admirabilis* sp. nov., here designated; the only species.

DIAGNOSIS. Clypeal medial lobe sharply prominent, with medial ridge. Lateral ocelli simple. Antennal bases covered dorsally by separate frontal prominences; male antenna 13-segmented; flagellomeres (except apical article) posteriorly with flat triangular prominences, mostly expressed on flagellomeres 5-9. Mandible short, curved forward, with inner preapical tooth. Palpi not elongate; palpal formula 6-4. Occipital carina forming a complete circle, almost touching hypostomal carina. Pronotal lobes almost touching tegulae. Pronotum posteriorly noticeably lower than upper scutal level. Adlateral lines reaching scutal posterior margin; admedial lines contiguous, longer than scutal length half. Mesopleuron with coarse episternal sulcus, scrobal sulcus, and precoxal carina; omaulus and sternaulus absent; intercoxal carina straight. Legs simple; hindcoxae contiguous; tarsal claws with a tooth. Propodeum without lateral carinae, with deep medial furrow posteriorly. Forewing marginal cell long and broad, with acute apex touching wing margin; three submarginal cells, II slightly larger than I, II more than twice as large as widened apically III; both recurrent veins received by submarginal cell II; veins M and RS slightly curved; forewing media diverging slightly beyond cu-a. Jugal lobe small, rounded; hindwing media diverging before cu-a. Abdomen with 7 visible segments, without separate petiole; abdominal sternite I with medial ridge, sternite II uniformly convex, without transverse basal concavity, sternite VII strongly tapered, thorn-shaped; tergite VII sharp, without pygidial plate; cerci absent.

COMPARISONS. The obvious prevalence of the second submarginal cell over the third is unusual for recent (and known fossil) Sphecidae and is found by way of an exception, for example, in the genera Podalonia Fernald, 1927 (Sphecinae, Ammophilini), Diploplectron W.Fox, 1893 (Astatinae, Astatini), Tachytella Brauns, 1906 (Crabroninae, Larrini), and Eremiasphecium Kohl, 1897 (Philanthinae, Eremiaspheciini). In all these cases, the second submarginal cell does not reach the size of the first submarginal cell and the marginal cell is always apically truncate (Diploplectron) or its apex does not touch the wing margin (the other genera), i.e., its diminution is associated with a general reduction in size of the distal forewing cells, including the marginal cell. The new genus, however, has a long marginal cell with its apex touching the wing margin, an enlarged second submarginal cell and a partly diminished third submarginal cell. Such reduction of the forewing venation, including only the distal part of the forewing submarginal cells, is presently unknown in recent Sphecidae.

Cirrosphex admirabilis sp. nov.

Figs 7-10

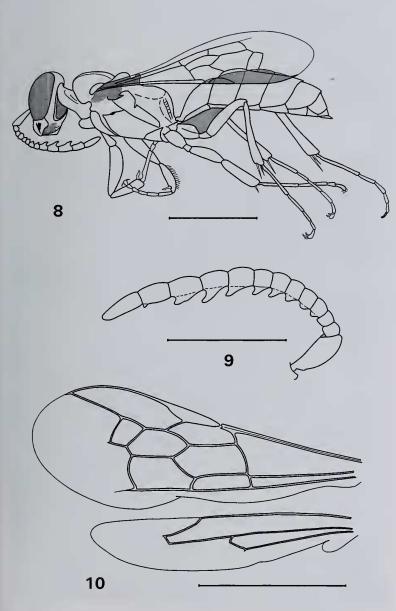
ETYMOLOGY. The species name *admirabilis* is derived from the Latin masculine adjective, meaning 'astonishing'; the name is a reference to the unusual form of the male antennae.

HOLOTYPE. Department of Palaeontology of The Natural History Museum (London), In.19125(1); completely preserved male specimen in a polished, flat, broadly ovate piece of Burmese amber (probably Upper Cretaceous).

DESCRIPTION. Male. Malar space short; occiput weakly expressed. Scape not more than twice as long as its maximum thickness; pedicellus almost round; flagellomeres 1–6 quadrate, 7–11 longer than wide, apical flagellomere 2.7 times longer than thick; flagellomeres 1–10 with flattened triangular prominences posteriorly, shortest at flagellomeres 1–4 and 10 and longest at flagellomeres 8–9. Frontal prominences above antennal sockets small, covering



Fig. 7 *Cirrosphex admirabilis* gen. et sp. nov., holotype, In.19125(1), male, Burmese amber. Length 3.5 mm.



Figs 8-10 Cirrosphex admirabilis gen. et sp. nov., holotype, In.19125(1), male, Burmese amber. 8, Total view laterally. 9, Left antenna laterally.
10, Left wings. Scale bars = 1 mm.

antennal bases dorsally from inside. Pronotal collar short, considerably lower than dorsal level of distinctly convex anteriorly scutum. Scutellum considerably roundly convex. Postscutellum short, strongly prominent medially. Mesopleuron convex, weakly sculptured, shiny. Dorsal part of metapleuron higher than 1/3 of its total height. Tarsomeres thin, cylindrical, without plantulae. Apical tarsomeres with small rounded arolium. Propodeal dorsal enclosure flat-concave, enclosed laterally with smooth furrows; propodeal hind side with deep medial furrow; propodeal spiracles oval, open. Abdomen somewhat elongate; tergite I from the base with lateral carinae, prolongly carinate; sternite I with medial ridge; tergite VII without pygidial plate, tapered apically; sternite VII strongly tapered, thornshaped.

Head anteriorly, scutum, scutellum, mesopleura ventrally, postscutellum, tergites V–VI, and sternites II–VI apically with distinct, erect pubescence, equal in length to lateral ocellus diameter or some longer at abdominal apex. Metapleuron, propodeum, and first abdominal segment bare. Foretibia and basitarsus with long, erect, and somewhat curved hairs.

Body length 3.5 mm. The female is unknown.

II. New tribes of the subfamily Ampulicinae

The only fossil ampulucine known so far, *Protodolichurus sucinus* Nemkov, 1988, was described from the Middle Eocene Baltic amber and was a representative of the tribe Dolichurini. Due to the characteristic features of short pronotum and unmodified abdominal sclerites, it was placed by Nemkov near the hypothetical ancestor of Dolichurini. A second species, *Trigonalys pervetus* Cockerell, 1917, from the Upper Cretaceous Burmese amber, was erroneously placed in the family Trigonalyidae. The Burmese amber collection at The Natural History Museum also contains four new species belonging to three new genera of Ampulicinae.

Subfamily **AMPULICINAE** 1. Tribe **APODOLICHURINI** nov.

TYPE GENUS. Apodolichurus gen. nov., here designated.

DIAGNOSTIC FEATURES.

- 1. Lower frons uniformly convex, without visible prominences.
- 2. Ocelli simple.
- 3. Palpi not elongate.
- 4. Female antennae 12-segmented, long and filiform; pedicel elongate, only slightly shorter than first flagellomere.
- 5. Pronotum elongate, with deep and wide medial concavity and more or less expressed lateral prolong prominences.
- 6. Mid- and hindcoxae separated.
- 7. Midtibia with two apical spurs.
- 8. Tarsomeres simple, with plantulae. Tarsal claws simple.
- 9. Forewing venation reduced: marginal cell very short, with anterior part shorter than stigma; enclosed submarginal and discoidal cells absent; submedial cell very short; forewing media diverging far beyond cu-a.
- 10. Hindwing jugal lobe small, rounded. Medial cell triangular. Hindwing media diverging considerably beyond cu-a.
- 11. Abdomen with 6 visible segments, without petiole, joined above hindcoxal bases.
- 12. Cerci absent.

COMPARISONS. The two representatives of the new tribe differ from other sphecids by the strong specialization of venation of both fore- and hindwings, expressing, firstly, the diminution of the marginal

cell and almost complete reduction of the submarginal, discoidal, and subdiscoidal cells, and secondly the proximal removal of only the externoposterior corner of the medial cell. Each of the features taken separately are found in various recent Sphecidae (acute and short marginal cell in Pemphredoninae, Ammoplanini; more or less disappearing submarginal, discoidal, and subdiscoidal cells in Crabroninae, Miscophini; almost triangular hindwing medial cell in Crabroninae, Crabronini). Simultaneous combination of these features is not found in any known recent or fossil Sphecidae. All the more, it is not found in Ampulicinae with their typically complete venation of both wings having minimum specialization. Another important (and unique) difference of the new tribe from all known Ampulicinae is the edentate tarsal claws. Finally, Apodolichurini trib. nov. differs from other Ampulicinae by its ovally elongate propodeum without distinct bend between dorsal and posterior parts and also by the spherical head and strongly elongate antennal pedicel (observable in only one of the species described below, the head was not preserved in the second species).

REMARKS. The reduction of the forewing venation is probably related to reduction of body size (maximum length of the discovered species is hardly more than 3.0 mm). At the same time, the characteristic shape of the pronotum, expressed adlateral lines, and two midtibial apical spurs allow the placement of both described species in the subfamily Ampulicinae.

Genus APODOLICHURUS nov.

ETYMOLOGY. The generic name is derived from the Greek prefix *apo*-, meaning 'from', and the generic name *Dolichurus*; it is masculine.

TYPE SPECIES. *Apodolichurus sphaerocephalus* sp. nov., here designated.

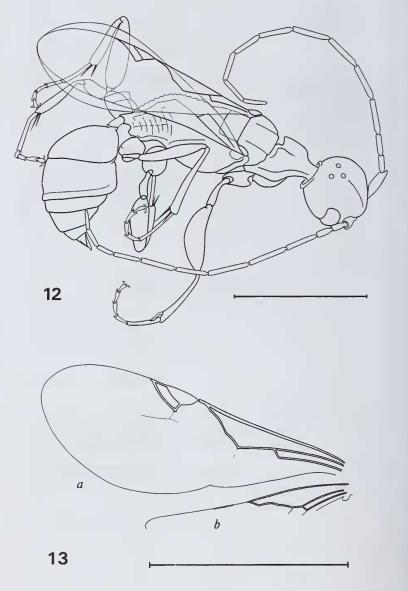
DIAGNOSIS. Head spherical; palpi not elongate; antennal sockets not covered by frontal prominences; antennae of female 12-segmented, long and filiform, with pedicel almost as long as 1st flagellomere; vertex roundly convex; occipital carina strongly developed, flat-widened ventrolaterally (ventral ends not visible). Pronotum distinctly longer than scutum; pronotal collar approximately as long as scutum, with two lateral ridges. Scutum transverse, with almost complete adlateral and weak admedial lines; scutellum flat, rectangular or trapeziform, transverse; postscutellum short; mesopleuron uniformly convex, with distinct episternal sulcus (other mesopleural sulci and carinae not expressed); intercoxal carina almost straight. Mid- and hindcoxae separate; femora thickened, tibiae and tarsi thin and long; tarsomeres simple, with apical plantulae ventrally (at least at right hindtarsomeres III-IV of the type species because other tarsi are visible only from external side); apical tarsomeres with weak arolium and edentate tarsal claws. Forewing marginal cell very short, with acute apex touching wing margin; submarginal, discoidal, and subdiscoidal cells absent; submedial cell very short, forewing media diverging far beyond cu-a. Hindwing medial cell almost triangular, media diverging beyond cu-a. Propodeum oval-elongate, with weakly developed lateral carinae, not bent between dorsal and hind sides, tubularly elongate apically. Abdominal tergite VI with medial ridge.

INCLUDED SPECIES. *Apodolichurus sphaerocephalus* sp. nov. and *A. diaphanus* sp. nov.

COMPARISONS. *Apodolichurus* gen. nov. resembles *Protodolichurus* only in the form of propodeum and some species of *Ampulex* in the



Fig. 11 Apodolichurus sphaerocephalus gen. et sp. nov., holotype, In.20150, female, Burmese amber. Length 3.1 mm.



Figs 12, 13 Apodolichurus sphaerocephalus gen. et sp. nov., holotype, In.20150, female, Burmese amber. **12**, Total view dorsolaterally. **13**, Left wings (a – forewing, b – anterior fragment of hindwing). Scale bars = 1 mm.

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form of pronotum. It differs from both recent and fossil genera of Ampulicinae by the tribal diagnostic features, particularly by the reduced forewing venation, principally different form of the hindwing medial cell, elongate antennal pedicel, and edentate tarsal claws.

Apodolichurus sphaerocephalus sp. nov. Figs 11–13

ETYMOLOGY. The species name is derived from the Greek nouns *sphaera*, meaning 'sphere', and *cephalon*, meaning 'head'; the name is a reference to the shape of the female head.

HOLOTYPE. Department of Palaeontology of The Natural History Museum (London), In.20150; completely preserved female specimen in a broad and flat wedge-shaped sample of Burmese amber (probably Upper Cretaceous), polished on one side, and containing numerous inclusions.

DESCRIPTION. Female. Head spherical; frons noticeably convex, slightly overgangling over antennal bases, with narrow medial furrow; eyes small; ocelli small, disposed in almost equilateral triangle; occipital carina laterally flattened and bent outside; antennae long and thin with cylindrical antennomeres. Pronotum with strongly developed, high, and pointed posteriorly prolong lateral ridges; scutum hardly convex, transverse; scutellum rectangular; trochanters (especially fore ones) thin and strongly elongate; femora (especially fore ones) noticeably bulbous ventrally; tibiae and tarsi thin, unmodified, only with short apical spines. Wings with very delicate and almost bare membrane; forewing without trace of Cu; hindwing with a long row of 10 small hamuli. Propodeum elongate, densely and uniformly transversely carinate laterally and posteriorly (invisible dorsally). Abdomen without petiole (first segment detached from propodeum and connected with it by stretched membrane), with



Fig. 14 Apodolichurus diaphanus gen. et sp. nov., holotype, In.19123(4), Burmese amber. Length 1.2 mm.

tergites almost completely covering sterna laterally; tergite VI sharp, with short medial carina.

Body very weakly sculptured: head dull, scutum delicately punctate and weakly shiny, abdomen microsculptured and weakly shiny. Pubescence practically absent.

Head black; rest parts of body (especially legs) considerably lighter – from brownish-red to amber-red; wing veins whitish-yellow.

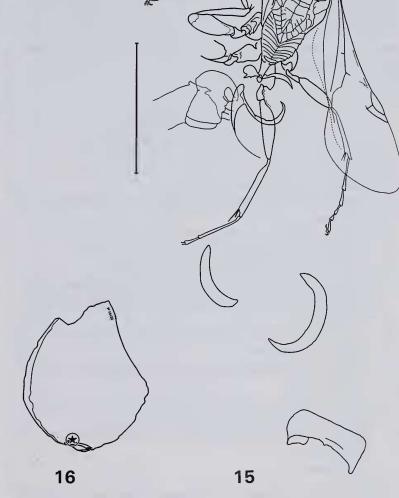
Body length 3.1 mm. The male is unknown.

REMARKS. It is likely that the abdomen of the specimen in its lifetime was weakly sclerotized; the sclerites are covered by numerous irregular, prolonged wrinkles.

Apodolichurus diaphanus sp. nov. Figs 14–16

ETYMOLOGY. The species name *diaphanus* is derived from the Latin masculine adjective, meaning 'translucent'; the name is a reference to the appearance of the body.

HOLOTYPE. Department of Palaeontology of The Natural History Museum (London), In.19123(4); partly preserved specimen of unknown sex (the following parts are absent: head, left midtarsus after the basitarsal proximal half, left hindleg after the femoral base, right



Figs 15, 16 Apodolichurus diaphanus gen. et sp. nov., holotype, In.19123(4), Burmese amber. 15, Total view dorsally (scale bar = 1 mm); 16, Position of holotype in amber sample In.19123.

foreleg, right hindtarsus after the 3rd tarsomere's base, left wings, and right hindwing, and apical abdominal segments; right forewing membrane is torn; sclerites of the abdominal segments I–III are separated) lying in the obtuse end (Fig. 16) of the irregularly ovate, flat, and broad wedge-shaped sample of Burmese amber (probably Upper Cretaceous) containing numerous inclusions.

DESCRIPTION. Sex unknown (head and abdomen apically absent). Pronotum with weakly prolonged and not angled posteriorly lateral ridges; scutellum trapeziform, narrowed posteriorly; trochanters not elongate; femora moderately thickened; tibiae and tarsi thin, unmodified, only apically with short spines. Forewing with thin trace of Cu. Propodeum uniformly narrowed towards apex; propodeal dorsal enclosure triangular, with thin medial and irregular lateral carinae, distinctly margined by broad transversely carinate concavity; propodeal hind side with thin medial ridge, densely and uniformly transversely carinate laterally. Abdominal sclerites separated (preserved only a few sclerites lying apart from the thorax).

Scutum delicately punctate, with moderately shiny interspaces. Abdominal sclerites almost unsculptured, weakly shiny.

Pubescence not expressed.

All preserved body fragments almost completely discoloured, translucent, amber-reddish; wing veins completely discoloured.

Body length 1.2 mm (without head and abdomen).

COMPARISONS. This species differs from *A. sphaerocephalus* sp. nov. by the considerably weaker lateral prominences of the pronotum, by simple trochanters, noticeably weaker bulbous femora, and by the distinct trace of the forewing Cu.

REMARKS. The translucence of the sclerites, absence of the head and the main part of the wings, and also separation of the abdominal sclerites lying separately far from the thorax, indicate that the fossilized specimen was not alive but already dead prior to entrapment, with almost or completely destroyed subcuticular structures, including intersegmental ligaments, muscles, and internal organs.

2. Tribe CRETAMPULICINI nov.

TYPE GENUS. Cretampulex gen. nov., here designated.

DIAGNOSTIC FEATURES.

- 1. Inner eye orbits parallel; ocelli simple.
- 2. Antennal sockets touching clypeal base; female antennae 12-segmented.
- 3. Clypeus uniformly convex, triangular, with medial carina.
- 4. Lower frons with prominence above each antenna.
- 5. Occipital carina expressed, at least dorsally.
- 6. Female mandibles hypognathous, straight, bidentate apically.
- 7. Palpi considerably elongate (maxillary palpi not shorter than head width).
- 8. Metasternum obtusely emarginate posteriorly, but not Y-shaped.
- 9. Hindcoxae separated.
- 10. Tarsomeres unmodified, without plantulae; tarsal claws with a ventral tooth.
- 11. Hindwing jugal lobe small, oval. Hindwing medial cell weakly elongate distally, with RS hardly longer than r-m.
- 12. Abdomen with 6 visible segments, with petiole inserted on level of hindcoxal bases.
- 13. Cerci absent.

COMPARISONS. Cretampulicini trib. nov. differs from all tribes of the subfamily Ampulicinae by the apically bidentate mandibles (unknown in Apodolichurini trib. nov. and *Trigampulex* gen. nov.), and from the recent tribes of the subfamily by the different form of the hindwing medial cell (RS hardly longer than r-m). Furthermore, Cretampulicini trib. nov. differs from the tribe Dolichurini by the sharp medial carina of the triangular clypeus, the separated hindcoxae, the absence of plantulae, and by the absence of a transverse concavity or carina on the abdominal sternite II. It differs from Ampulicini by the elongate palpi, moderately emarginate but not Y-shaped metasternum, and unmodified tarsi. Cretampulicini trib. nov. differs from Apodolichurini trib. nov. by the pair of lower frontal prominences above the antennal bases, elongate palpi, dentate tarsal claws, complete forewing venation, and by the ovally elongate hindwing jugal lobe. It differs from Mendampulicini trib. nov. by the pair of lower frontal prominences above the antennal bases, simple eyes, and by the triangular clypeus with a sharp medial carina. Finally, it differs from Trigampulex gen. nov. by the complete forewing venation (the discoidal cell II completely developed, trace of the forewing 1r absent, recurrent vein I received by the submarginal cell II), elongate propodeum, and by the developed abdominal petiole.

It differs from Ampulicini by the marginal cell apex touching the wing margin

Genus CRETAMPULEX nov.

ETYMOLOGY. The generic name is derived from the Latin masculine adjective *cretaceus*, indicating the age of the specimen, and the generic name *Ampulex*. It is masculine.

TYPE SPECIES. *Cretampulex gracilis* sp. nov., here designated; the only species.

DIAGNOSIS. Clypeus triangular with sharp medial carina; lower frons with a pair of small prominences, hardly covering antennal sockets above; vertex simple; eyes unmodified, with parallel inner orbits; ocelli simple; occipital carina distinct, at least dorsally (ventral part of head invisible); mandibles hypognathous, slightly curved apically, with small inner preapical tooth; palpi elongate, maxillary palpi hardly shorter than head width; palpal formula 6-4; antennae long and slender, 12-segmented in female. Pronotum elongate, with pronotal collar concave medially and with sharp lateral ridges; scutum convex (insufficiently visible from above); mesopleuron weakly convex; episternal sulcus thin; omaulus, scrobal sulcus, acetabular carina, subomaulus, and sternaulus not expressed; precoxal carina distinct, slightly continuing on mesopleuron; scutellum flat, short; postscutellum convex, short; metasternum emarginate posteriorly, but not Y-shaped; mid- and hindcoxae separated; legs long and slender, with unmodified tarsomeres; plantulae absent; arolium small, tarsal claws with a tooth. Forewing marginal cell with acute apex touching wing margin, 1.5 times longer than stigma; three submarginal cells: I largest; II trapeziform, narrowed anteriorly (though 1r absent), 1.5 times narrower than I, 1st transverse submarginal vein angulately curved; submarginal cell III almost rectangular, 1.5 times narrower but longer than II; two discoidal cells: recurrent vein I received by submarginal cell II, recurrent vein II - by submarginal cell III; forewing media diverging beyond cu-a. Hindwing with a row of 7 hamuli; RS short, almost equal to r-m; angle between RS and r-m obtuse; hindwing media diverging at cu-a; jugal lobe elongate, approximately equal to 1/3 of submedial cell length. Propodeum long, distinctly bent between dorsal and hind sides; hind part margined by sharp carinae from all sides; lateral carinae not expressed. Abdomen with thin petiole, inserted on level of hindcoxal bases, and with unmodified segments II-VI; tergite VI conical, without pygidial plate, but with thin medial carina.

COMPARISONS. *Cretampulex* gen. nov. differs from all recent and known fossil genera of Ampulicinae by the apically bidentate man-

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dibles and comparatively small number of hamuli. Among recent genera it resembles Aphelotoma Westwood, 1841 and Austrotoma Riek, 1955 in having the separated lower frontal prominences, differing from them by the medially carinate triangular clypeus, apically bidentate mandibles, elongate palpi, strong lateral ridges of the pronotal collar, absence of the omaulus, sternaulus, tarsal plantulae, and forewing vein 1r, by the narrow forewing submarginal cell III and the relative positions of the recurrent veins, and by the developed hindwing jugal lobe and the abdominal petiole. Among fossil representatives of the subfamily, Cretampulex gen. nov. resembles Protodolichurus in having the separated lower frontal prominences, the medially carinate clypeus, and similar forewing venation, differing from it by the triangular clypeus, longer pronotum with the expressed lateral ridges of its collar, absence of tarsal plantulae and forewing vein 1r, by the narrow submarginal cell III, the form of the hindwing medial cell and confluent cu-a, by the distinct bend between the propodeal dorsal and hind sides, and by the distinct abdominal petiole.

Cretampulex gracilis sp. nov.

Figs 17–20

ETYMOLOGY. The species name is derived from the Latin masculine adjective *gracilis*, meaning 'slender'; the name is a reference to the shape of the female body.

HOLOTYPE. Department of Palaeontology of The Natural History Museum (London), In. 19123(5); completely preserved female specimen lying in the centre (Fig. 20) of the polished from the both sides, irregularly ovate, flat, and broad wedge-shaped sample of Burmese amber (probably Upper Cretaceous), containing numerous inclusions.

DESCRIPTION. Female. Head oval, higher than wide; clypeus triangular, with distinct medial carina; frons weakly convex, with narrow medial furrow; separated frontal prominences small, covering antennal sockets above from inside; malar space longer than maximum scape thickness; vertex weakly and uniformly convex; ocelli small, forming an obtuse-angled triangle; oculo-ocellar distance longer than that between lateral ocelli; occipital carina expressed at least dorsally and laterally (ventral part of head invisible); antennal sockets touching clypeal base; mandible rather thin and somewhat widened apically, with weakly curved inside apical and shorter inner preapical teeth; antenna long and slender, with unmodified flagellomeres at least thrice as long as thick, last article rounded apically; palpi distinctly elongate, maxillary palpi not shorter than head width. Pronotum elongate, with medial concavity and distinct, acute-angled dorsoposteriorly lateral ridges; scutum uniformly convex (thorax and propodeum invisible dorsally); mesopleuron with distinct episternal sulcus and some concave prolonged lines (probably, their part may be the result of deformation, but not real sulci); legs practically unmodified, without outer tibial spines, but with short ventral bristles on tarsomeres, most distinct on foretarsus. Propodeum elongate, bent between dorsal and hind sides. Abdomen with distinct petiole (it's detailed structure invisible), with tergites considerably covering sternites laterally; tergite VI sharp-conical, with thin medial carina (prolongly split apically, with right apical part turned up); sting thin and straight.

Body sculpture weak, expressed as moderate punctures at frons and scutal visible part, with weakly shiny interspaces; abdomen microstriate, shiny.

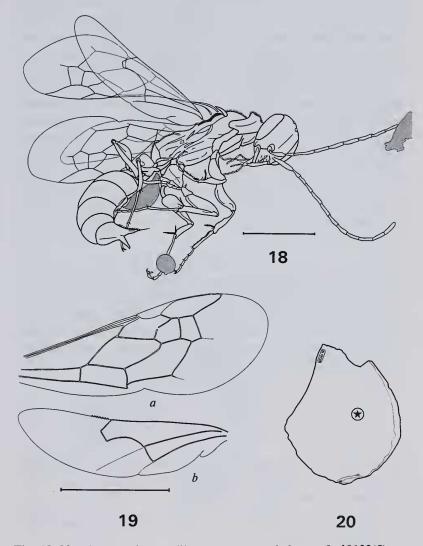
Clypeus with sparse erect bristles; pronotal lateral ridges, scutum and propodeum at least dorsally, and lower margin of abdominal tergite VI covered with dense erect hairs.

Body more or less uniformly darkened (probably, brownish-black); wing veins dark-brown; palpi and tarsi somewhat lighter than body.

Body length 3.7 mm. The male is unknown.



Fig. 17 *Cretampulex gracilis* gen. et sp. nov., holotype, In.19123(5), female, Burmese amber. Length 3.7 mm.



Figs 18–20 Cretampulex gracilis gen. et sp. nov., holotype, In.19123(5), female, Burmese amber. 18, Total view ventrolaterally. 19, Wings (a – left forewing, b – right hindwing). 20, Position of holotype in amber sample In.19123. Scale bars = 1 mm.

3. Tribe MENDAMPULICINI nov.

TYPE GENUS. Mendampulex gen. nov., here designated.

DIAGNOSTIC FEATURES.

- 1. Mandibular sockets open, united with oral fossa.
- 2. Clypeus uniformly convex, not carinate medially.
- 3. Lower frons with unpaired prominence.
- 4. Occipital carina forming a complete circle, considerably separated from hypostomal carina.
- 5. Mandible hypognathous, crescent.
- 6. Palpi considerably elongate.
- 7. Metasternum emarginate posteriorly, but not Y-shaped.
- 8. Mid- and hindcoxae separated.
- 9. Tarsomeres unmodified.
- 10. Abdominal petiole inserted between and on same level as hindcoxae.

COMPARISONS. This new tribe is characterized by the presence of the characters listed above, which are typical to the Ampulicinae. It differs from all other tribes by the long crescent mandibles, comparatively small eyes, and the occipital carina forming a complete circle (in the studied specimens of Apodolichurini trib. nov. and Cretampulicini trib. nov. the occipital carina is visible only dorsally, and it is unknown for Trigampulex gen. nov. because of the absence of the holotype head). Furthermore, Mendampulicini trib. nov. differs from Dolichurini by the separated hindcoxae and the abdominal petiole inserted between and on the same level as the hindcoxae; from Ampulicini by the clypeus without a medial carina, unpaired frontal prominence, open mandibular sockets, hypognathous mandibles, considerably elongate maxillary and labial palpi, thin and unmodified tarsomeres (without ventral pubescence on the penultimate tarsomeres and with an arolium on the apical tarsomeres), not Y-shaped metasternum, and by the fore- and hindwing mediae diverging beyond cu-a; from Apodolichurini trib. nov. by the considerably flattened head, pronotal collar without expressed lateral ridges, long scutum, and by the dentate tarsal claws; from Cretampulicini trib. nov. by the clypeus lacking a medial carina, unpaired frontal prominence, strongly developed vertex, undeveloped lateral ridges of the pronotal collar, hindwing media diverging beyond cu-a, and by undeveloped hindwing jugal lobe; from Trigampulex gen. nov. by the hindwing media diverging beyond cu-a and by the petiolate abdomen.

REMARKS. Mendampulicini trib. nov. resembles Dolichurini, at least the genus *Trirogma*, by the main diagnostic features (trapezifom clypeus without medial carina, unpaired frontal prominence, elongate palpi, and unmodified tarsi). The crescent mandibles, the flattened head with a complete occipital carina and small eyes, and the hindwing media diverging beyond cu-a testify to the high specialization of the fossil specimen and separate it from other ampulicine tribes.

Genus MENDAMPULEX nov.

ETYMOLOGY. The generic name is derived from the Latin masculine adjective *mendax*, meaning 'false', and the generic name *Ampulex*. It is masculine.

TYPE SPECIES. *Mendampulex monilicularis* sp. nov., here designated; the only species.

DIAGNOSIS. Clypeus trapeziform, with uniformly convex surface and without medial carina; lower frons with obtuse-angulately carinate frontal prominence hardly covering dorsally antennal sockets;



Fig. 21 *Mendampulex monilicularis* gen. et sp. nov., holotype, In.20711, female, Burmese amber. Length 4.7 mm.

vertex considerably elongate; eyes small, strongly convex, with strongly curved inner orbits; ocelli simple; occipital carina distinct, forming a complete circle, separated from hypostomal carina; mandible hypognathous, long, crescent, with small outer external preapical notch and inner triangular apical tooth; maxillary palpi not shorter than head height, labial palpi also elongate; palpal formula 6-4; antennae long and slender, 12-segmented. Pronotum elongate, with collar slightly broader than long, with medial concavity, and sharply margined laterally; scutum flat, rectangular, slightly longer than pronotal collar, with complete adlateral and hardly expressed admedial lines; mesopleuron convex; episternal sulcus coarse and broad; omaulus, scrobal sulcus, and acetabular carina not expressed; subomaulus and sternaulus absent; precoxal carina strongly developed, not continuing on mesopleuron; scutellum flat, square; postscutellum convex, short; metasternum emarginate posteriorly, not Y-shaped; mid- and hindcoxae separated. Legs long and slender, with unmodified tarsomeres; ventral plantulae absent; arolium small, sharp apically; tarsal claws thin and long, with a tooth near apex. Fore- and hindwing mediae diverging beyond cu-a; hindwing jugal lobe not expressed. Propodeum long, abrupt posteriorly, with Ushaped dorsal enclosure, margined laterally and posteriorly by sharp ridges. Abdominal petiole inserted on level of hindcoxal bases.

COMPARISONS. *Mendampulex* gen. nov. resembles *Trirogma*, *Paradolichurus* Williams, 1960, and *Dolichurus* Latreille, 1809 in having the unpaired, though weaker frontal prominence, but differs from them by the stronger separated antennal sockets, longer pronotum, and by the fore- and hindwing mediae diverging beyond cu-a. Furthermore, *Mendampulex* gen. nov. differs from the first genus by the long palpi and undeveloped omaulus, scrobal sulcus, and sternaulus; from the second by the undeveloped omaulus and by the tarsi without plantulae; and from the last by the trapeziform clypeus, undeveloped omaulus, scrobal sulcus, sternaulus, acetabular carina, and by the tarsi without plantulae.

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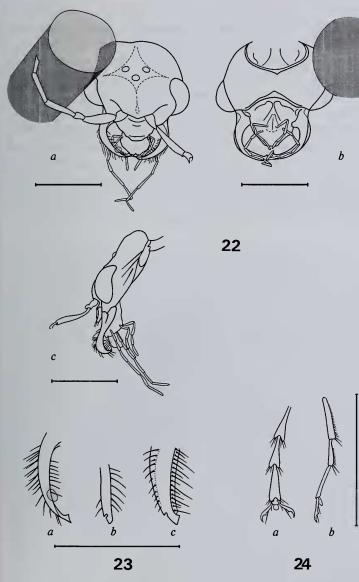
Mendampulex monilicularis sp. nov.

ETYMOLOGY. The species name is derived from the Latin neuter noun *monile*, meaning 'beads, necklace', and a diminutive suffix *-culum*; the name is a reference to the position of the specimen inside the small bead.

Figs 21-25

HOLOTYPE. Department of Palaeontology of The Natural History Museum (London), In.20711; partly preserved female specimen (the following parts are absent: left flagellomeres 1–10 and right flagellomeres 3–4, left foretarsomeres II–V, left midtarsus, both hindlegs after coxae, wings after submedial cell, and abdomen after petiole) in an almost spherically polished bead of Burmese amber (probably Upper Cretaceous).

DESCRIPTION. Female. Head considerably flattened, with strongly developed vertex; clypeus trapeziform, roundly truncate apically, with obtuse angles laterally; frons flat-convex, ocellar triangle slightly concave; medial ocellus larger than lateral one; eyes small and convex, almost twice as high as distance between inner orbits dorsally; oculo-ocellar distance approximately twice as long as that between lateral ocelli; malar space not longer than lateral ocellar diameter; occipital carina separating from hypostomal farther than





Figs 22–24 Mendampulex monilicularis gen. et sp. nov., holotype, In.20711, female, Burmese amber. **22**, Head (a – anteriorly, b – posteriorly, c – laterally). **23**, Mandibles apically (a – right, frontally, b – left, ventrally, c – left, posteroventrally). **24**, Left foretarsomeres III–V (a – dorsally, b – laterally). Scale bars = 1 mm.

Fig. 25 *Mendampulex monilicularis* gen. et sp. nov., holotype, In.20711, female, Burmese amber; total view (*a* – dorsally, *b* – ventrally, *c* – laterally); scale bars = 1 mm.

Clypeal apical margin and external and inner margins of mandible with rows of long erect bristles, those 1.5–2.0 times as long as thickness of mandibular mid part; pro- and mesothorax mainly covered with very short, directed backwards, appressed hairs practically hiding dull and inpunctate surface; precoxal carina posteriorly with longer and also directed backwards dense bristles; tarsomeres I–IV ventrally with rows of dense short bristles and sparser and longer thin ventral (mainly on tarsomere I) and apical spines; apical tarsomere practically bare ventrally.

Body mainly dark-brownish, without separate spots; head completely, mandibles basally and apically, apical half of scapes, foretibiae apically, midcoxae, and mesopleura posteriorly black; midfemora and tibiae mainly yellow.

Body length 4.7 mm (without abdomen). The male is unknown.

III. A new genus of Sphecidae

Genus TRIGAMPULEX nov., incertae sedis

ETYMOLOGY. The generic name is derived from the generic names *Trigonalys* and *Ampulex*. It is masculine.

TYPE SPECIES. *Trigonalys pervetus* Cockerell, 1917, here designated; the only species.

DIAGNOSIS. Postscutellum short. Propodeum rounded, without distinctly margined dorsal enclosure and visible lateral carinae. Legs weakly modified: femora shorter than corresponding tibiae; midtibia with two apical spurs and sparse short spines outside; tarsi elongate, with apical tarsomere connected with apex of unmodified penultimate tarsomere; plantulae absent; tarsal claws with a tooth. Forewing with three submarginal cells and one discoidal cell (discoidal cell II rudimentary, margined from outside and posteriorly by scarcely visible traces of veins 2m-cu and Cu₁). Hindwing medial cell with RS almost perpendicular to R1. Abdomen sessile, petiole undeveloped.

COMPARISONS. Based on the peculiarities of the forewing venation (recurrent vein I received by submarginal cell I and trace of the recurrent vein II received by submarginal cell III; medial cell weakly elongate), *T.pervetus* may be attributed to either the family Trigonalyidae or to the Sphecidae.

The simple trochanters of the mid- and hindlegs, the midtibiae with two apical spurs, the absence of the plantulae at the apices of the unmodified tarsomeres, the tooth claws, the developed cleaning brush of the inner hindtibial spur and hind basitarsus, the weakly developed costal cells of both wings, the distinct trace of vein 1r in the forewings, the outer prolong veins (M-a and Cu₁-a of the foreand RS-a, M-a, Cu-a, and A₁-a of the hindwings) ending far from the wing margin, the forewing media diverging distinctly beyond cu-a, the distinctly separated hindwing jugal lobe, and the single row of hamuli suggest a placement outside of Trigonalyidae (where it was originally placed by Cockerell, 1917b), but is suggestive of Sphecidae, perhaps of the subfamily Ampulicinae.

Trigampulex pervetus differs from the representatives of Ampulicinae by the distinctly diminished forewing submarginal cell

III, by the reduced outer veins of the forewing discoidal cell II (2m-cu and Cu₁), and by the form of the hindwing medial cell (RS almost perpendicular to R1). The last two features also place *T.pervetus* separately from all Sphecidae, but the inaccessibility for study of many important characteristics of the structure of the head and thorax (first of all, of the mesothorax) does not allow to interpret definitely this species as the representative of a separate subfamily. I therefore place the fossil as *incertae sedis* near Ampulicinae until new, more perfectly preserved material, is discovered.

Trigampulex pervetus (Cockerell, 1917), comb.nov. Figs 26–31

1917 Trigonalys pervetus Cockerell: 79, fig. 1 (Trigonalidae).

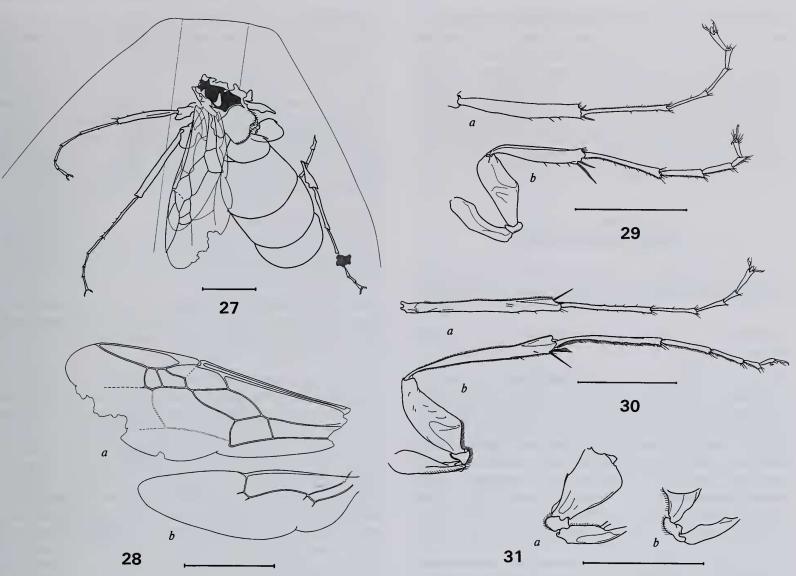
HOLOTYPE. Department of Palaeontology of The Natural History Museum (London), In.19093; partly preserved specimen of unknown sex (the following parts are absent: head, prothorax including forelegs, scutum and scutellum, right wings completely and left wings basally, right midleg from apical half of femur to basitarsus, right hindleg from apical half of femur to tibial middle, and abdominal segments after segment IV; legs and propodeum considerably deformed) in a spindle-shaped polished bead of Burmese amber (probably Upper Cretaceous).

DESCRIPTION. Sex unknown (head, prothorax, and abdomen apically lost). Preserved parts of mesopleura strongly deformed, with vague structure; postscutellum (left part preserved) short; legs very slender: femora (especially hind ones) distinctly shorter than corresponding tibiae; midtibiae ventrally in middle and hindtibiae basally obtuse-angled; tarsomeres very long, tarsomere I almost equal to corresponding tibia, apical tarsomere longer than penultimate one. Propodeum rounded (though strongly deformed, right up to the cuticular ruptures, those Cockerell has, probably, interpreted as bilobed scutellum). Abdomen, in comparison with wings and thorax, large, sessile; tergite I considerably smaller than each of the rest segments, especially tergite II.

Coxae, trochanters, and partly femora covered ventrally with



Fig. 26 *Trigampulex pervetus* (Cockerell), holotype, In.19093, Burmese amber. 20. Total view dorsally. Length 3.4 mm.



Figs 27-31 Trigampulex pervetus (Cockerell), holotype, In. 19093, Burmese amber. 27, total view dorsally; 28, left wings (a – forewing, b – hindwing);
29, Left midleg (a – tibia and tarsus dorsally, b – laterally). 30, Left hindleg (a – tibia and tarsus dorsally, b – laterally). 31, Right coxa, trochanter, and base of femur laterally (a – hindleg, b – midleg). Scale bars = 1 mm.

short and dense erect hairs; mid- and hindtibiae with some ventral bristles, the last also with short and dense erect hairs; tarsomeres I– IV with similar hairs, apical tarsomeres bare; propodeum covered with longer, but sparser erect hairs; abdominal sclerites practically bare, visibly transversely microstriate, shiny.

Body completely black; wing veins from black to brown; midtibiae reddish basally.

Body length 4.0 mm (without head, anterior part of thorax, and abdominal apex), forewing length 3.4 mm.

IV. New genera of the subfamily Pemphredoninae

The subfamily Pemphredoninae is the most numerous group of sphecids in the fossil record at various ages: the genus *Passaloecus* Shuckard, 1838 includes Miocene *P.scudderi* Cockerell 1906, *P.fasciatus* Rohwer, 1909, and *P.munax* Sorg, 1986, Eocene *P.microceras* Sorg, 1986, and Middle Eocene *P.zherichini* Budrys, 1993, *P.piletskisi* Budrys, 1993, and *P.electrobius* Budrys, 1993; the genus *Eoxyloecus* Budrys, 1993 – Middle Eocene *E.albipalpis* Budrys, 1993, *E.palionisi* Budrys, 1993, *E.setipes* Budrys, 1993, and *E.succinicola* Budrys, 1993; the genus *Eopinoecus* Budrys, 1993 – Also Middle Eocene *E.samogiticus* Budrys, 1993 and *E.truncifrons* Budrys, 1993. The monotypic Middle Eocene genera *Succinoecus*

Budrys, 1993, *Palanga* Budrys, 1993, and *Eomimesa* Budrys, 1993 include *S.lituanicus* Budrys, 1993, *P.sucinea* Budrys, 1993, and *E.rasnitsyni* Budrys, 1993.

Only three of the described species belong to the Upper Cretaceous: *Lisponema singularis* Evans, 1969 (Cedar Lake amber), *Pittoecus pauper* Evans, 1973, and *Cretoecus spinicoxa* Budrys, 1993 (last two species from Taimyr amber). The majority of the described genera may be undoubtedly attributed to the subtribe Pemphredonina of the Pemphredonini (sensu Bohart and Menke, 1976), excluding *Eomimesa* (Psenini, Psenina). The positions of the remaining genera are not as clear.

For example, the status of the genus *Palanga* (lacking a prominent between the antennae clypeal medial lobe, but having a complete occipital carina, ecarinate pronotal collar, long adlateral lines, areolate episternal sulcus, complete forewing venation, and developed pygidial plate) with respect to *Spilomena* Shuckard, 1838 and *Arpactophilus* Smith, 1863 is of some doubt. Furthermore, though *Palanga* has 5-segmented maxillary palpi (judging from the original description, but 6-segmented judging from the personal communication of Dr. David Grimaldi – American Museum of Natural History, New York, USA), these are not shortened as in Spilomenina (sensu Menke, 1989).

Similar difficulties exist for the genus Eopinoecus and, to an even

greater degree, for *Lisponema*. If the first really resembles *Passaloecus*, differing only in the absence of the forewing recurrent vein II (may be a result of specialization, that was not kept by recent representatives of the group), then the truncate forewing marginal cell and the weakly dentate tarsal claws of *Lisponema* isolate this genus from all Pemphredoninae, excluding extremely specialized Ammoplanini. Unfortunately, the holotype of *Lisponema* is headless and its mesopleura are not described. Additional investigations are necessary for ascertaining the relationships of *Palanga* and *Lisponema* with recent groups of Pemphredoninae.

Tribe **PEMPHREDONINI** 1. Genus *PROLEMISTUS* nov.

ETYMOLOGY. The generic name is derived from the Latin prefix *pro*-, meaning 'before', and the generic name *Polemistus*. It is masculine.

TYPE SPECIES. *Prolemistus apiformis* sp. nov., here designated; the only species.

DIAGNOSIS. Clypeus (partly visible) short; lower frons considerably convex, with distinct anteroventral edge covering antennal bases; inner eye orbits almost parallel; ocelli simple, placing in obtuse-angled triangle; occipital carina interrupted, not reaching hypostomal carina; mandible without inner teeth and ventral notch or prominence, with two apical teeth (lower tooth longer than upper one); palpal formula 6-4; female antenna 12-segmented, with all segments longer than thick. Pronotum with short collar, bearing transverse carina; scutum with hardly visible short premedial lines and short traces of adlateral lines; episternal sulcus distinctly expressed (ventral ends invisible); scrobal sulcus distinct; omaulus, subomaulus, acetabular carina, sternaulus, and hypersternaulus absent; precoxal carina developed laterally and ventrally, but not continuing on mesopleuron; midcoxae contiguous; fore- and midtrochanters longer than half of corresponding femora; fore- and midfemora bulbous ventrally, hindfemur triangularly broadened anteriorly in basal 1/3; midtibia bulbous apically, with one apical spur; foretarsal rake and plantulae absent, tarsal claws simple, arolium distinct. Forewing marginal cell long, with acute apex reaching wing outer angle, at least twice as long as not enlarged stigma; two submarginal cells: submarginal cell I hardly shorter than marginal cell, submarginal cell II approximately thrice as short as marginal cell; two discoidal cells: discoidal cell I hardly longer than stigma, discoidal cell II slightly shorter than submarginal cell I; recurrent vein I received by middle of submarginal cell I, recurrent vein II received by proximal 1/3 of submarginal cell II; forewing media diverging beyond cu-a. Hindwing (hardly visible) with short, rounded jugal lobe, not longer than half of submedial cell; hindwing media diverging before cu-a. Propodeum short, with appressed, but not margined dorsal enclosure, with distinct lateral carinae. First abdominal segment with short (shorter that wide) petiole, consisting of sternite I; tergite VI rounded, without pygidial plate or medial carina.

COMPARISONS. Single midtibial spur, short abdominal petiole consisting of sternite I, and simple tarsal claws allow placement of this specimen into the subfamily Pemphredoninae, and the characteristic forewing venation to the tribe Pemphredonini. Among described fossil pemphredonine genera, *Prolemistus* gen. nov. resembles *Succinoecus* in the absence of the hypersternaulus, but differs from it by the apically bidentate mandibles, distinct transverse carinate pronotal collar, simple and thin scrobal and episternal sulci, and by the lack of even a trace of the hypersternaulus. Among recent pemphredonine genera *Prolemistus* gen. nov. most closely resembles *Passaloecus* and *Polemistus* Saussure, 1892 by having an uninterrupted episternal sulcus and by lacking the pygidial plate and outer hindtibial spines. The new genus differs from *Passaloecus* in the absence of the omaulus, and from *Polemistus* by the wide head with practically parallel inner eye orbits and the elongate flagellomeres. *Prolemistus* gen. nov. also differs from both genera by the absence of the hypersternaulus, and from all mentioned genera by the ventrally interrupted occipital carina with the prominent roundly triangular ventral angles, distinctly prominent lower frons overhanging the antennal bases, and by the obtusely broadened hindfemora.

Prolemistus apiformis sp. nov.

Figs 32-34

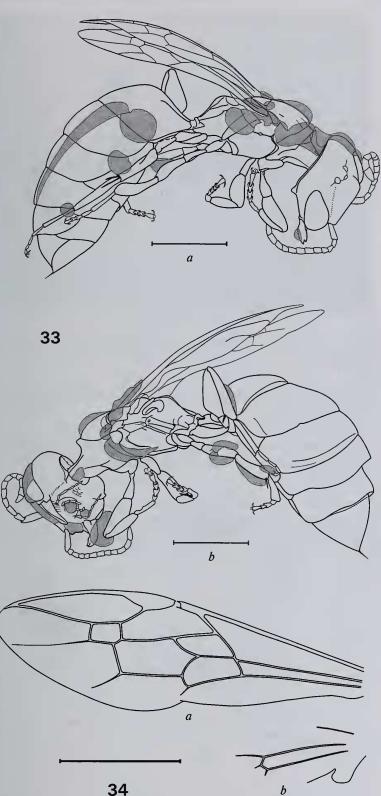
ETYMOLOGY. Species name is derived from the Latin masculine adjective *apiformis*, meaning 'bee-shaped'; the name is a reference to the shape of the female body.

HOLOTYPE. Department of Palaeontology of The Natural History Museum (London), In.20181; completely preserved female specimen in a polished irregularly oval sample of Burmese amber (probably Upper Cretaceous).

DESCRIPTION. Female. Head considerably widened and thickened; clypeus invisible, but probably short; malar space shorter than forebasitarsal thickness; frons strongly convex, overhanging antennal bases; eyes convex, with inner orbits parallel or slightly converging below; ocelli placing in obtuse-angled triangle, medial ocellus smaller than lateral one; oculo-ocellar distance strongly longer than that between lateral ocelli; occipital carina interrupted ventrally, with prominent lower angles, placing from hypostomal carina at distance, distinctly longer than mandibular base width; mandible widened in middle, with two apical teeth (outer tooth longer than inner one); middle flagellomeres 1.2–1.5 times as long as their maximum thickness, without prominences. Pronotal collar with almost right lateral angles, distinctly margined anteriorly and laterally, approximately 1.5 times longer than antennal thickness; scutum flat-convex;



Fig. 32 *Prolemistus apiformis* gen. et sp. nov, holotype, In.20181, female, Burmese amber. Length 5.1 mm.



Figs 33, 34 Prolemistus apiformis gen. et sp. nov, holotype, In.20181, female, Burmese amber. 33, Total view (a – dorsolaterally, b – ventrolaterally). 34, Left wings (a – forewing, b – basal fragment of hindwing). Scale bars = 1 mm.

scutellum flat; mesopleuron moderately convex; postscutellum visibly convex. Tarsomeres unmodified, without plantulae; apical tarsomere with small arolium. Propodeum short, with dorsal side somewhat concave and shorter than hind side; lateral carinae distinct.

Body sculpture weak, hardly visible on head; scutum, mesopleura, and propodeal lateral sides not sculptured, weakly shiny; scutellum dull.

Body pubescence weak, very short, mainly appressed with simple light hairs, expressed mainly on temples and abdominal tergites. Body uniformly coloured, black or dark-brown, except somewhat lighter palpi.

Body length 5.1 mm. Male unknown.

REMARKS. Though the holotype specimen is completely preserved, it is strongly deformed owing to compression. As a result, it appears from some angles that the scutum bears adlateral lines and the left basitarsus is flattened. In fact, however, it concerns only the left side, where the midcoxa, midfemur, mid basitarsus are also, if not more strongly so, compressed laterally and clasped to the flattened abdomen together with the left hindtarsus. The right mid- and hindtarsomeres are not flattened.

2. Genus CRETOSPILOMENA nov.

ETYMOLOGY. The generic name is derived from the Latin masculine adjective *cretaceus*, indicating the age of the specimens, and the generic name *Spilomena*. It is feminine.

TYPE SPECIES. *Cretospilomena familiaris* sp. nov., here designated, the only species.

DIAGNOSIS. Clypeus (partly visible) short, distinctly roundly convex (visible in paratypes 3 and 7); frons flat; inner eye orbits almost parallel; lateral ocelli simple (visible in holotype); occipital carina expressed at least dorsally and laterally (visible in holotype and paratypes 4 and 5); mandible without inner teeth and ventral notch or prominence, bidentate apically (visible in paratype 7); palpal formula 6-4, palpal segments very short (visible in paratype 3); female antenna 12-segmented, all articles longer than maximum thick. Pronotal collar elongate, with transverse carina; scutum with hardly visible short adlateral lines; mesopleuron with expressed episternal sulcus (visible in holotype and paratype 4); scrobal sulcus, sternaulus, hypersternaulus, omaulus, subomaulus, and acetabular carina not expressed; midcoxae contiguous; legs unmodified, tibiae without outer spines; midtibia with one apical spur; tarsomeres with short apical spines; ventral plantulae and foretarsal rake absent; tarsal claws simple, arolium hardly visible. Forewing marginal cell considerably wide, with acute apex touching wing margin, approximately 1.5 times as long as distinctly enlarged stigma; two submarginal cells: submarginal cell I hardly shorter, submarginal cell II approximately thrice shorter than marginal cell; single discoidal cell 1.5 times longer than stigma; recurrent vein received by submarginal cell I; forewing media diverging beyond cu-a. Hindwing media diverging at cu-a, RS practically straight and equal to r-m (visible in paratype 1); hindwing with 5 long hamuli. Propodeal dorsal enclosure flattened and weakly margined laterally, bearing a pair of premedial carenulae; propodeum with strong sharp posterolateral thorns, joining posteriorly by transverse carina; propodeal lateral carinae not expressed distinctly. First abdominal segment with elongate (slightly longer than wide) petiole, consisting of tergite I and sternite I; tergite VI rounded, with short apicomedial carina (visible in paratype 1), without pygidial plate.

COMPARISONS. The single midtibial apical spur, the simple tarsal claws, the mesopleuron without sulci (except the episternal sulcus), the reduced forewing venation, the enlarged stigma, and the short abdominal petiole consisting of tergite I and sternite I allow the placement of *Cretospilomena* gen. nov. into the tribe Pemphredonini of the subfamily Pemphredoninae. It is difficult to place this genus into any of the subtribes of Pemphredonini that have an unmodified marginal, two submarginal, and single discoidal cells (Menke, 1989), because the specimen combines features of both Stigmina (6-segmented maxillary palpi) and Spilomenina (shortened palpal segments

and a short abdominal petiole consisting of both tergite I and sternite I).

In outward appearance *Cretospilomena* gen. nov. most closely resembles *Microstigmus* Docke, 1907 while the forewings resembles those of *Spilomena*. In the main features of the forewing venation (distinctly enlarged stigma, not reduced marginal, two submarginal, and single discoidal cells) the genus is similar to *Lisponema* and *Eopinoecus* among fossil genera, and to *Spilomena* among recent genera.

Lisponema differs from Cretospilomena gen. nov. by the truncate marginal cell with veins 3r and RS-a, by the more strongly developed adlateral lines, deep and prolongly carinate prescutellar furrow, weakly dentate (judging from the original description) tarsal claws, weak posterolateral propodeal angles, and by the non-petiolate abdomen. Eopinoecus, also having the palpal formula 6-4, differs from Cretospilomena gen. nov. by the supraantennal frontal tubercle, apically truncate and delimited by lateral teeth medial clypeal lobe, apically tridentate mandibles, distinctly areolate scrobal and episternal sulci bearing a trace of the hypersternaulus, weakly enlarged stigma, hindwing media diverging before cu-a, densely areolate propodeum without posterolateral thorns, and by the flat and short pygidial plate. Both Lisponema and Eopinoecus also differ from Cretospilomena gen. nov. by the following features: the narrow pronotal collar and the group of 6 hamuli on the hindwing anterior margin. Spilomena differs from Cretospilomena gen. nov. by the absence of the occipital carina and sharp posterolateral propodeal thorns, palpal formula 5-4, and the non-petiolate abdomen.

Cretospilomena familiaris sp. nov.

Figs 35-45

ETYMOLOGY. Species name is derived from the Latin feminine adjective *familiaris*, meaning 'family'; the name is a reference to the probable collective nesting.

HOLOTYPE. Department of Palaeontology of The Natural History Museum (London), In.19136(1); completely preserved female specimen (Figs 35, 39), in the narrow part (Fig. 38) of a flat-oviform polished sample of Burmese amber (probably Upper Cretaceous).

DESCRIPTION. Female. Head flattened; upper frons weakly convex, without expressed medial furrow; inner eye orbits parallel; malar space shorter than antennal thickness; vertex and temples uniformly moderately convex, without angles; mandible unmodified, bidentate apically, outer tooth rather longer than inner one; flagellomeres slightly longer than thick, apical flagellomere distinctly longer than penultimate one. Pronotum distinctly elongate; pronotal collar at least twice as long as scape maximum thickness, with straight transverse carina not reaching pronotal lobes laterally; scutum roundly convex, without visible prolong lines, distinctly arched above level of pronotal collar; prescutellar furrow thick, ecarinate prolongly; scutellum flat, trapeziform; postscutellum equal or hardly longer than scape thickness; mesopleuron uniformly convex, with weak, thin, and curved episternal sulcus between pronotal lobe and forecoxal base; legs unmodified, slender, without foretarsal rake and tibial spines; plantulae absent; tarsal claws simple, slightly widened basally; hindwing anterior margin with distal group of 5 rather long and weakly curved hamuli (hindwing bases invisible). Propodeal dorsal enclosure flat, with a pair of straight premedial carinae not reaching its apex, distinctly separated from hind side by straight transverse carina ending laterally with sharp thorns. First abdominal segment narrowed anteriorly forming a petiole consisting of both tergite I and sternite I; tergite VI with distinct medial carina, but without long erect bristles.

Head dull, with vague sculpture; scutum uniformly and delicately



Fig. 35 *Cretospilomena familiaris* gen. et sp. nov., holotype, In.19136(1), female, Burmese amber. Length 2.3 mm.

punctate, with shiny interspaces; abdomen without distinct sculpture, weakly shiny.

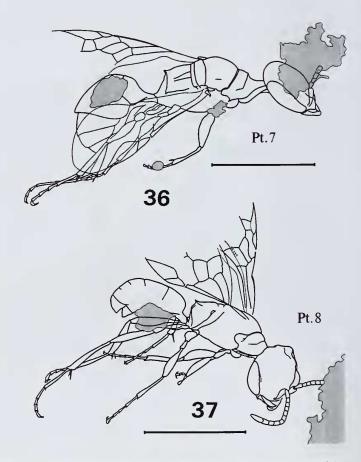
Body pubescence very weak and short, hardly visible.

Head and thorax black; mandibles (except dark apices), palpi, antennae, abdomen, and legs from brownish-red to red.

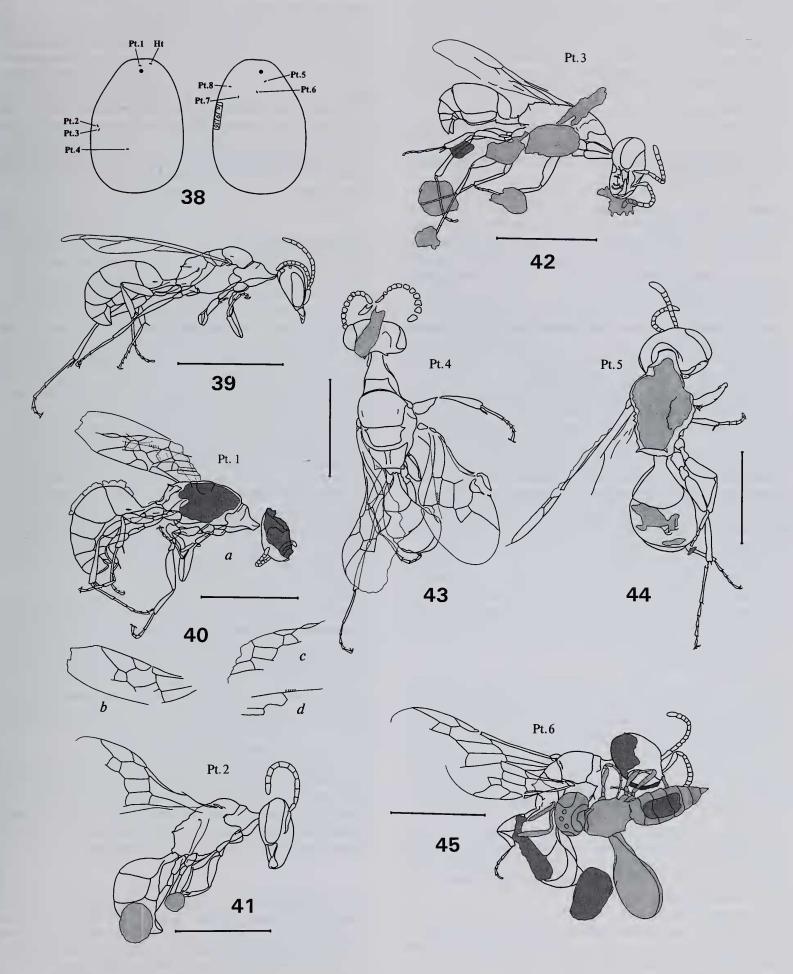
Body length 2.3 mm.

PARATYPES. Eight females in various states of preservation, all in the same piece of amber as the holotype (In.19136):

Paratype 1 (Fig. 40), In.19136 (2). Head anteriorly (including



Figs 36, 37 *Cretospilomena familiaris* gen. et sp. nov., females. 36, Paratype 7, In.19136(8), total view dorsolaterally. 37, Paratype 8, In.19136(9), total view laterally. Scale bars = 1 mm.



Figs 38-45 Cretospilomena familiaris gen. et sp. nov., females. 38, Position of types in Burmese amber sample In.19136. 39, Holotype, In.19136(1), total view laterally. 40, Paratype 1, In.19136(2), (a – total view laterally, b – left forewing, c – fragment of right forewing, d – fragment of right hindwing). 41, Paratype 2, In.19136(3), total view ventrolaterally. 42, Paratype 3, In.19136(4), total view ventrolaterally. 43, Paratype 4, In.19136(4), total view dorsally. 44, Paratype 5, In.19136(6), total view dorsally. 45, Paratype 6, In.19136(7), total view dorsolaterally. Scale bars = 1 mm.

frons, eyes, and clypeus) and thorax laterally considerably destroyed; both fore- and right hindwing basally, distal parts of right fore- and hindwings, and also left hindwing completely absent; abdominal tergites I and II flattened laterally. Body length 2.6 mm.

Paratype 2 (Fig. 41), In.19136 (3). Left antenna, right hindwing, and right forewing basally absent; left pair of wings and mesopleural structure invisible; legs and abdomen partly covered with foreign particles. Body length 2.3 mm.

Paratype 3 (Fig. 42), In.19136 (4). Right pair of wings folded prolongly; structure of thorax laterally and of propodeum invisible; tarsi, mesopleura, and partly right antenna covered with foreign particles. Body length 2.4 mm.

Paratype 4 (Fig. 43), In.19136 (5). Following parts visibly deformed: antennae (articles separated), pronotal anterior part (unusually elongate), and wings (anterior veins curved up to rupture of right stigma, vein between Sc+R and RS, and couplings between wing, tegula, and thorax); only anterior part of right hindwing with a row of 5 hamuli visible; head dorsally covered with foreign particles. Body length 2.7 mm.

Paratype 5 (Fig. 44), In.19136 (6). Mesothorax together with right pair of wings and propodeum dorsally almost completely, prothorax dorsally from right side, and left pair of wings mainly destroyed during polishing the sample; abdominal tergite II with large concavities, mainly anteriorly. Body length 2.5 mm.

Paratype 6 (Fig. 45), In.19136 (7). Both hindwings and forewings distal membranes invisible; thorax laterally including legs hidden under well preserved specimen of Scelionidae; abdominal tergite I and apex covered with foreign particles; head and abdominal tergites I–III strongly concave dorsally. Body length 2.4 mm.

Paratype 7 (Fig. 36), In.19136 (8). Mesopleural structure, hindwings, right forewing distal membrane, and the main part of veins of right forewing invisible; head anteriorly covered with foreign particle; abdominal tergite I apically and tergite II basally destroyed. Body length 2.5 mm.

Paratype 8 (Fig. 37), In.19136 (9). Structure of frons, mesopleura, lateral sides of abdomen, and forewings distal membranes invisible; right forewing submarginal cell II absent; only anterior part of left hindwing with a row of 5 hamuli visible; left antenna apically, abdomen ventrally in the middle, and hindfemora partly covered with foreign particles. Body length 2.2 mm.

The male is unknown.

REMARKS. This is the only known case of the simultaneous preservation of a large group of sphecid wasps belonging to one species in a fossil resin. I propose that this fact may suggest the compact nesting of several females in a small biotope, as is observed among some recent xylobiotic species of the genus *Spilomena*, and was probably typical for *C.familiaris* sp. nov., if it was not an eusocial mode of life, similar to that of the genera *Microstigmus* (Matthews, 1968a, 1968b) or *Arpactophilus* (Matthews & Naumann, 1988).

DISCUSSION. The multiplicity of the representatives of the tribe Pemphredonini discovered in fossil resins of various ages, including Upper Cretaceous amber, testifies to the earlier isolation of this specialized group of sphecid wasps and to the establishment of its close association with arboreal plants.

A comparative analysis of fossils of various ages demonstrates that the Upper Cretaceous representatives of the tribe already had the characteristic outward appearance, including the wing venation (at least of the forewings), and were characterized by a set of specialized features. These include the apically truncate marginal cell (*Lisponema*), the strongly convex lower frons covering the antennal bases from above (*Prolemistus*), the sharp posterolateral thorns of the propodeum (*Cretospilomena*), the more or less well developed teeth of the tarsal claws (*Pittoecus, Lisponema*), and the shortened 6-segmented maxillary palpi (*Cretospilomena*).

If the last two features are archaic, then the truncate marginal cell, the strongly convex lower frons, and the strongly developed propodeal thorns are not present in both later and recent fossil Pemphredonini. They should be recognized as lost specializations which were specific to genera. The absent or weakly developed prolonged mesopleural sulci (especially the hypersternaulus) and the nonareolate episternal sulcus in the genera *Cretoceus*, *Pittoecus*, and *Prolemistus*, should probably also be considered plesiomorphic.

The simultaneous fossilization of many females of *C.familiaris* sp. nov. is of special interest. I think, this unique case may show the early evolution of sociality in Pemphredonini.

CONCLUSIONS

Study of the present material suggests that the evolution of the Upper Cretaceous Sphecidae, in contrast to the recent representatives of the family, had specific pecularities. As well as such generalized features as the completely developed adlateral lines and two apical midtibial spurs (the shortened hindwing RS in the majority of the studied forms is probably also a generalized feature), they have acquired some apomorphies, that are not present in recent sphecid wasps. The unique structure of the scape and the wing venation of Burmastatus, the pectinate antennae and the venation of the forewing submarginal sector of Cirrosphex, the spherical head, the reduced forewing venation, and the edentate tarsal claws of Apodolichurus, the reduced discoidal cell II of Trigampulex, as well as, probably, the ventrally angulate mandibles of Burmastatus, the small eyes, complete occipital carina, and specialized mandibles of Mendampulex, the apically bidentate mandibles of Cretampulex, the strongly convex lower frons of Prolemistus, and the dentate laterally propodeum of Cretospilomena should be placed into the group of such features.

Differences such as general shift of the forewing veins and cells to the wing proximal half and the diminution of the marginal cell in *Burmastatus*, the diminution of the forewing submarginal cell III with simultaneous enlarging of the marginal cell in *Cirrosphex* are of interest, because they do not conform to the general directions of the venational reductions that are characteristic for recent representatives of the family (truncation or separation of the forewing marginal cell apex with its diminution, reduction of the forewing submarginal sector mainly by the diminution of the submarginal cell II or by junction of the submarginal cells I–II or II–III).

It is apparent that the Upper Cretaceous fauna of sphecid wasps was sufficiently variable and differed considerably from the recent representatives of the family by possessing many specialized features, including a different evolutionary development of the wing venation. All mentioned pecularities of the discovered taxa place them far from the hypothetical ancestor of recent Sphecidae.

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